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RESEARCH ARTICLE

What are the main local drivers determining richness and fishery yields in tropical coastal fish assemblages?

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ABSTRACT. Seasonal ecological effects caused by temperature and photoperiod are typically considered minimal in the tropics. Nevertheless, annual climate cycles may still influence the distribution and abundance of tropical species. Here, we investigate whether seasonal patterns of precipitation and wind speed influence the structure of coastal fish assemblages and fishing yields in northeast Brazil. Research trips were conducted during the rainy and dry seasons using commercial boats and gear to sample the fish community. Diversity was analyzed using abundance Whittaker curves, diversity profiles and the Shannon index. Principal Component Analysis (PCA) was used to analyze associations between the abundance of species and various environmental variables related to seasonality. A total of 2,373 fish were collected, representing 73 species from 34 families – 20 of which were classified as both frequent and abundant. Species richness was greater and more equitable during the rainy season than the dry season – driven by changes in the precipitation rather than to wind speed. Species diversity profiles were slightly greater during the rainy season than the dry season, but this difference was not statistically significant. Using PCA was identified three groups of species: the first associated with wind speed, the second with precipitation, and the third with a wide range of sampling environments. This latter group was the largest and most ecologically heterogeneous. We conclude that tropical coastal fish assemblages are largely influenced by local variables, and seasonally mediated by annual changes related to precipitation intensity and wind speed, which in turn influences fishery yields.

KEY WORDS. artisanal fishing, fishes, wind, precipitation, seasonality, gillnet.

INTRODUCTION

Water quality and nutrient availability in coastal waters are influenced by environmental factors such as the spatial and temporal patterns of precipitation, land drainage, and wind patterns (Kennedy et al. 2002). Seasonal changes in biophysical factors can modify the composition of communities, affecting the occurrence and distribution of species within and between trophic levels (Blaber et al. 1995, Brown et al. 1997, Walther et al. 2002). In coastal ecosystems, these effects are usually mediated through temporal changes in temperature profile, the extent and magnitude of precipitation and continental runoff, wind patterns and storm frequency (Bernal-Ramírez et al. 2003, Jury 2011, Kennedy et al. 2002). Studies on the effects of changes in climate and biological productivity in the eastern Atlantic have documented a range of seasonal effects on trophic levels, coral reefs, juvenile dispersal, fishery yields and fish species abundance (e.g. Muehe and Garcez 2005, Ciotti et al. 2010, Costa et al. 2010, Leão et al. 2010, Schroeder and Castello 2010). Even so, the generalization of these findings is not possible as climate and local landscape characteristics may drive communities to different profiles.

In the tropics, where annual changes in temperature and photoperiod are minimal, seasonality is heavily determined by precipitation (Lowe-McConnell 1987), which generates dry and rainy seasons (Figueroa and Nobre 1990). Such seasonal variation, though less apparent than that observed in temperate areas, has the capacity to influence fish behavior (Wootton 1990) and, consequently, may influence the distribution and abundance of species within a given area (Laevastu and Hayes 1981) with a knock-on effect on fishery yields (Hilborn and Walters 1992). The consequences of these variability includes the estuarization process, when coastal waters resembles estuarine conditions (Longhurst and Pauly 1987b), even affecting the functional diversity of fish assemblages (Passos et al. 2016).

Even facing those large-scale patterns, local effects are detectable after higher scale effects being known and considered.

In this study, the objectives were to determine how seasonal patterns of precipitation and wind influence the temporal structure of tropical fish assemblages and the yields of the coastal gillnet fishery.

MATERIAL AND METHODS

Samples were collected in the central coastal zone of the state of Alagoas, north-eastern Brazil, near the main regional fisheries harbor (Fig. 1).

The seasonal patterns are typically tropical and consist of a rainy season from March to August and a dry season from September to February (Macêdo et al. 2004). Precipitation is high on the coastal plain; with an annual average of 1,800 mm. Coastal currents are conditioned by winds and tides and, in the rainy season, trade winds. During the rainy season, the southeast quadrant (SE) experiences more frequent and intense winds, while during the dry season, such winds flow from the northeast quadrant (NE) (Araújo et al. 2006).

Trips were made on crescent moon days in an 8 m wooden boat with an ice capacity of 500 kg and a one-cylinder, diesel-powered B18 engine. Six sampling trips were conducted between October 2010 to August 2011, with three occurring during the rainy season (June/July/August) and three during the dry season (October/December/February). Each trip lasted three days, totaling 30 launches of effective fishing.

Sets were established between two fishing areas with mud and gravel substrates, known locally as "Lama Grande" and "Tira da Pedra" (Fig. 1). The first set was approximately 11 km from Jaraguá Harbor at a depth of approximately 12 m; the second was located approximately 14 km from the port of Jaraguá in a depth of approximately 20 m. The distance between the centroids of the sites was approximately 6.5 km.

A commercial gillnet 1,330 m long and 1.5 m high was used, with a mesh size of 40 mm between opposite knots and a nylon thread size of 50 mm. Gillnets were set near the surface parallel to the seabed and was fixed at both ends with anchors. The mean ± standard deviation of the duration of each set was 3.51 ± 1.01 hours.

For each launch, the set position and duration were recorded, wind direction and intensity, the type and number of each species caught and the total length (cm) of each fish caught. All fishes were physically anesthetized by hypothermia on board and killed freezing on ice.

Additional data on precipitation, wind speed and direction were obtained from INMET/SEMARH, Brazilian government. To facilitate the communication of our results to environmental managers and members of local communities, a scale of wind intensity was created based on the reports of the fishermen on board and the daily wind speed recorded by INMET/SEMARH as follows: null = 0.0 m/s; weak ≤ 3.0 m/s; strong > 3.0 m/s. Similarly, the precipitation values recorded by INMET/SEMARH were categorized as very low = 0–31 mm; low = 32–84 mm; moderate = 85–137 mm; moderate-high = 138–196 mm; high = 197–200 mm and very high ≥ 201 mm.

From these data, there was calculated: the number of species and specimens per set, the mean length per species per

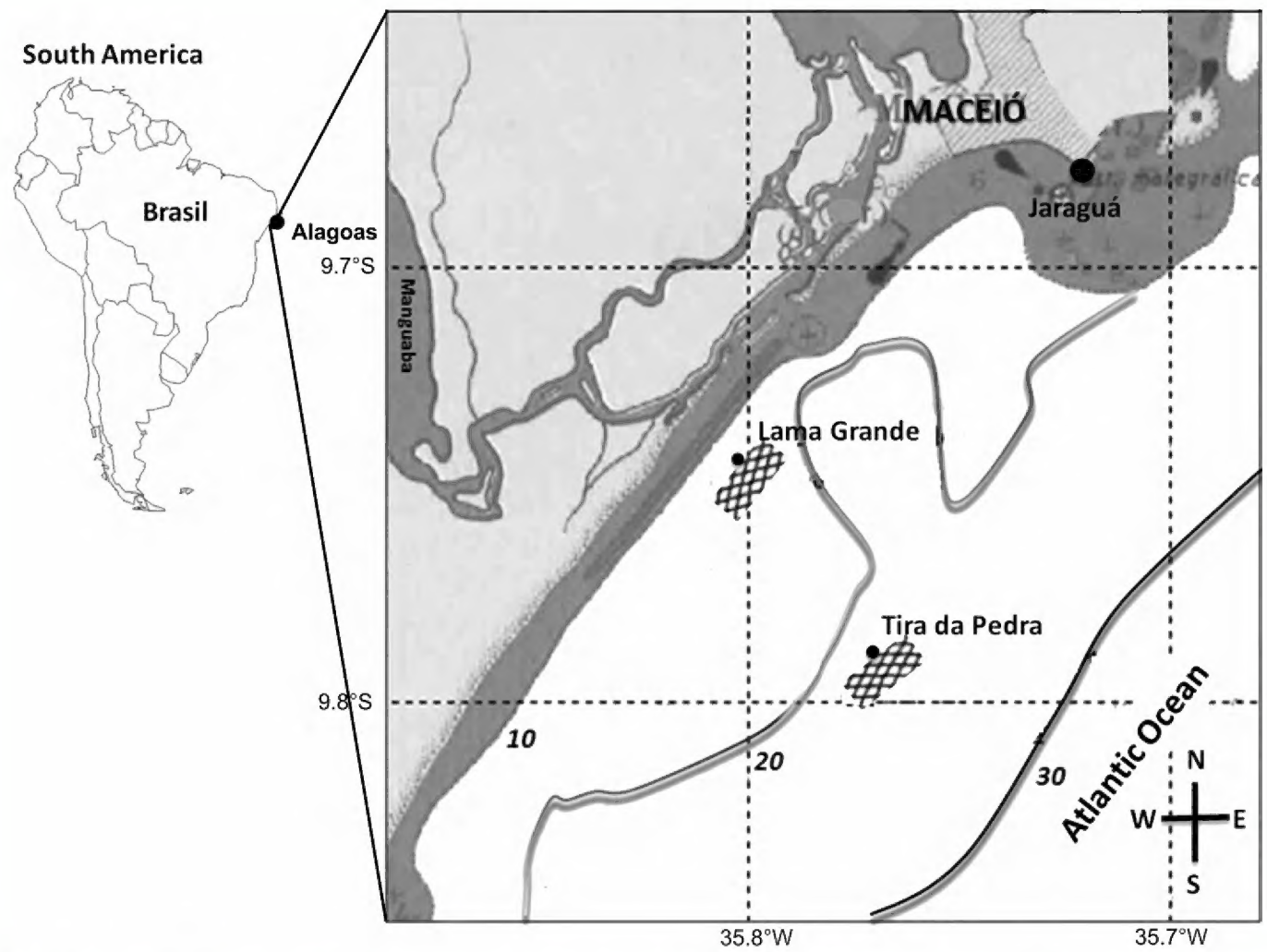


Figure 1. Location of the sampled area within the Alagoas coast. Jaraguá fishing harbor and the fishery sites were indicated.

set, the catch per set (kg), the CPUE (catch per unit effort) with standardized effort (1,330 m gillnet * set hours), the mean wind speed in m/s (mean of 6 hours per day: 3 hours before + 2 hours during the set + 1 hour after) and the total monthly precipitation (mm). All data were compared between the dry and rainy seasons.

Data analysis

Samples of all species were taken to the laboratory (SISBIO 1837810) after each fishing trip and identified using a variety of keys (Lessa and Nóbrega 2000, Menezes and Figueiredo 1980). One or two type specimens of each species were placed in a standard collection as reference material (see Suppl. material 1).

Analyses of diversity were conducted using three different methods: Whittaker abundance curves (Whittaker 1960, Whittaker et al. 2001), diversity profiles (Melo 2008) using Rényi series – Eq. (B.1) (Magurran 2004) and the Shannon-Wiener diversity index (H') – Eq. (B.2), including a bias correction term (Hammer et al. 2001). A modified t-test was used to analyze the Shannon index, estimating the variance by Eq. (B.3) (Magurran 2004). Diversity analyses were conducted using the program PAST (Hammer et al. 2001).

Variables were analyzed by univariate and factorial analyses of variance (ANOVA). The frequency of wind direction during the surveys was analyzed using the chi-square test (Legendre and Legendre 1998). Univariate and factorial analyses were performed in Statistica v.8.

The classification of abundant and frequent species by season was based on numerical abundance (PN %) and the frequency of occurrence (FO %), and the classification included four categories (Garcia and Sobrinho 2001): 1) Abundant and common (PN % > 100/S and BF % ≥ 50 %), where S is the total number of species per season; 2) Abundant but uncommon (PN % > 100 I/O and FO % < 50 %); 3) Sparse but common (PN % < 100/S and BF % ≥ 50 %); 4) Sparse and uncommon or occasional (PN % < 100/S and FO % < 50 %).

Because the variables used in the exploratory analysis were all quantitative and linear, a Principal Component Analysis (PCA) was performed (Legendre and Legendre 1998). To facilitate the PCA and focus on species of high commercial value, there were selected 16 species from the most abundant and frequent species and included precipitation and wind speed data. The multivariate model was tested by analysis of similarity (ANOSIM), and groups were identified by the greatest influence test SIMPER (Similarity Percentage) using Bray Curtis distance index (Clarke 1993). Multivariate analysis was performed using Statistica v. 8 and tests were done in PAST.

RESULTS

Diversity

There were collected 2,373 fishes representing 73 species and 34 families (Suppl. material 1). From these species, there were 39 categorized as abundant but uncommon, 51 as occasional species, and 51 and 20 as abundant and common species, respectively (the same species can belong to more than one category depending on the weather station) (Suppl. material 1). The frequent and abundant species, from most to least abundant, were as follows: Carangidae: *Caranx crysos* (Mitchill, 1815) (blue runner) (N = 360); Sciaenidae: *Larimus breviceps* Cuvier, 1830 (shorthead drum) (N = 321); Scombridae: *Euthynnus alletteratus* (Rafinesque, 1810) (little tunny) (N = 301); Scombridae: *Scomberomorus brasiliensis* Collette Russo & Zavala-Camin, 1978 (serra spanish mackerel) (N = 254); Haemulidae: *Conodon nobilis* (Linnaeus, 1758) (barred grunt) (N = 168); Clupeidae: *Opisthonema oglinum* (Lesueur, 1818) (Atlantic thread herring) (N = 108); Carangidae: *Chloroscombrus chrysurus* (Linnaeus, 1766) (Atlantic bumper) (N = 98), Sciaenidae: *Menticirrhus littoralis* (Holbrook, 1847) (gulf kingcroaker) (N = 72); Ariidae: *Bagre bagre* (Linnaeus, 1766) (coconut sea catfish) (N = 57); Lutjanidae: *Lutjanus synagris* (Linnaeus, 1758) (lane snapper) (N = 56); Ariidae: *Cathorops spixii* (Agassiz, 1829) (madamango sea catfish) (N = 51); Carangidae: *Caranx hippos* (Linnaeus, 1766) (jack crevalle) (N = 50); Sciaenidae: *Macrodon ancylodon* (Bloch & Schneider, 1801) (king weakfish) (N = 42); Centropomidae: *Centropomus parallelus* Poey, 1860 (fat snook) (N = 41); Haemulidae: *Haemulopsis corvinaeformis* (Steindachner, 1868) (roughneck grunt) (N = 40) and Engraulidae: *Cetengraulis edentulus* (Cuvier, 1829) (atlantic anchoveta) (N = 35). Among these 20 species, seven were prevalent during the rainy season and three in the dry season (Suppl. material 1). Rarefaction curves estimated for the samples caught during dry and rain seasons using the bootstrap richness estimator yield different patterns of relative diversity for both seasons for all sample sizes (Fig. 2). Although the dry season richness is closer at high sample size, the asymptotic level was reached for both seasons and the difference remained.

The size and slope of the curves in the Whittaker abundance diagram indicated that the rainy season (Fig. 3) had greater species richness and equitability than the dry season (Fig. 4). In the rainy season, the predominant species in order of decreasing abundance were *C. crysos*, *E. alletteratus*, *S. brasiliensis* and *L. breviceps*. Apart from these species, abundance decreased gradually with increasing richness. In the dry season, the predominant species were *L. breviceps*, *C. nobilis*, *C. chrysurus* and *C. crysos*.

The diversity profiles indicated that diversity was marginally higher in the rainy season than in the dry season. The relevant alpha values are close to one indicating greater abundance. Diversity varied more in richness than in abundance between seasons (Fig. 5). However, the Shannon diversity index did not differ between seasons (t–test, $p > 0.05$).

Interaction of physical and biological variables

The univariate ANOVA showed significant differences between season in the number of species, number of fish, CPUE and mean species length (Tab. 1). The highest average observed values were observed in the rainy season (Fig. 6).

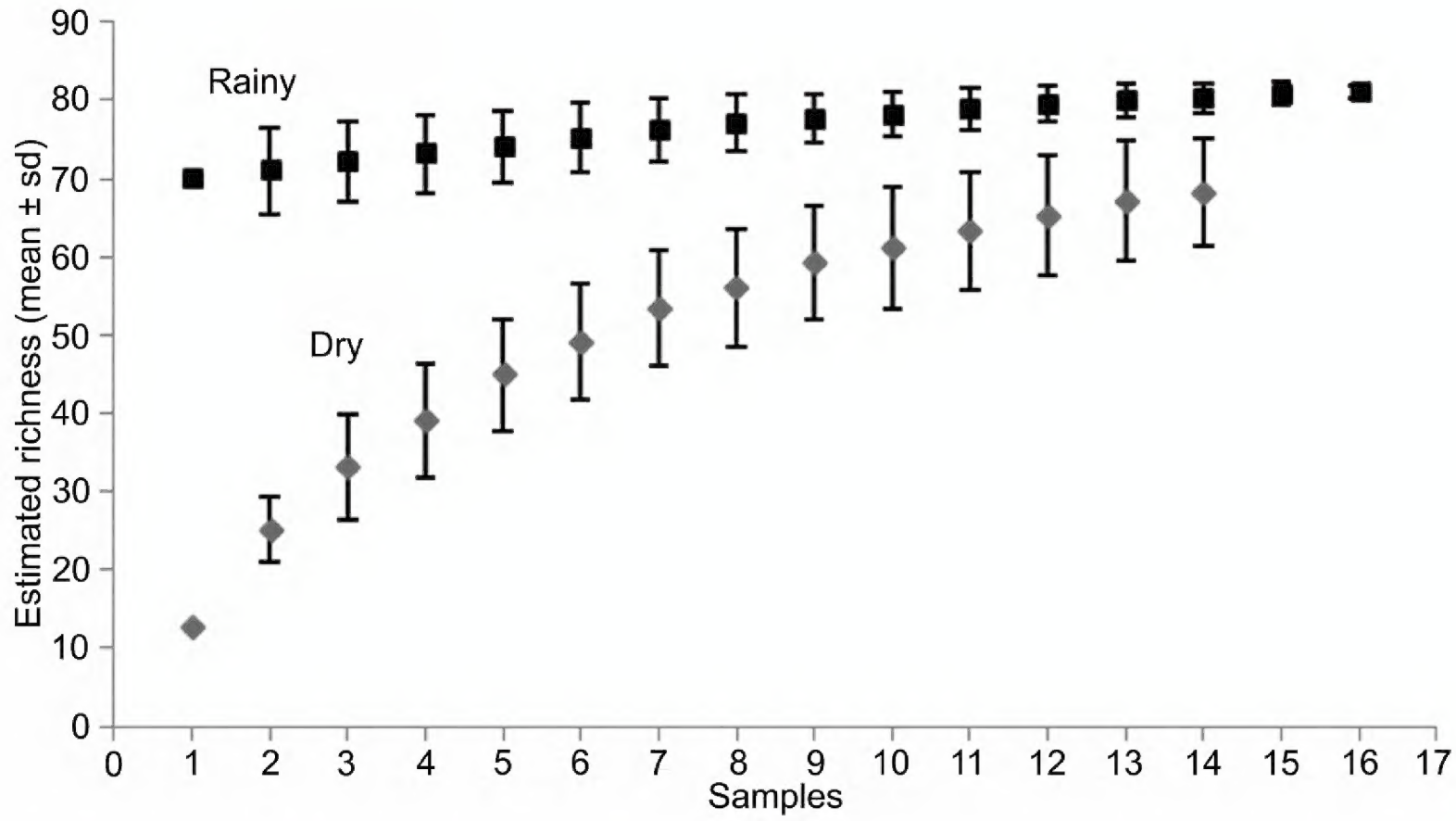


Figure 2. Rarefaction curves for the samples caught during dry and rain seasons using the bootstrap richness estimator.

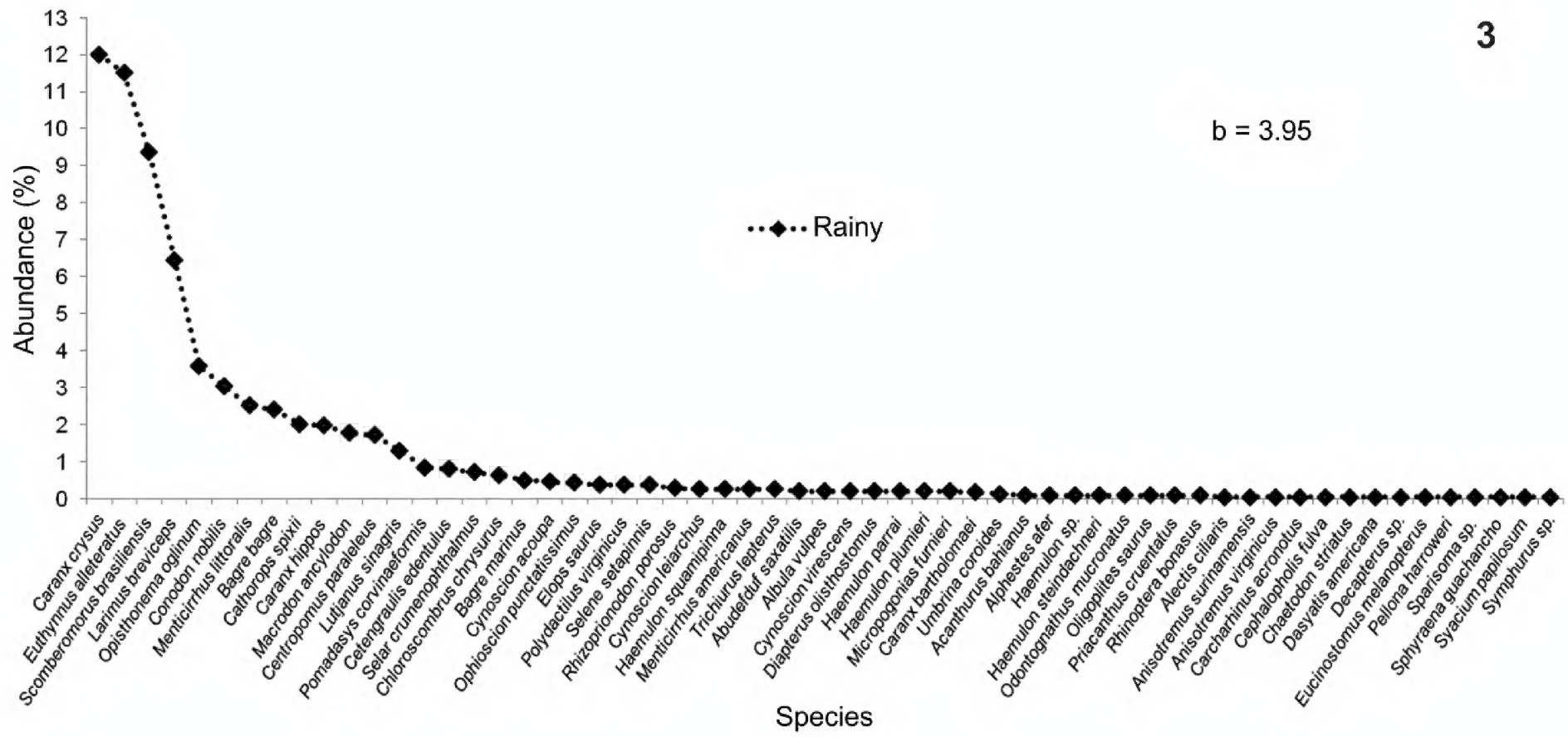
Table 1. Analysis of variance tables to compare seasonal effects on species number, number of fishes, CPUE and mean length for fishes caught at the coast of Alagoas.

Effect	df	SS	MS	F	p
Species number					
Intercept	1	4392.30	4392.30	276.58	<0.01
Season	1	208.03	208.03	13.10	<0.01
Error	28	444.67	15.88		
Total	29	652.70			
Number of fishes					
Intercept	1	187704.30	187704.30	73.28	<0.01
Season	1	28644.30	28644.30	11.18	<0.01
Error	28	71716.40	2561.30		
Total	29	100360.70			
CPUE (Kg)/(m*h)					
Intercept	1	0.00	0.00	51.53	<0.01
Season	1	0.00	0.00	8.02	0.01
Error	28	0.00	0.00		
Total	29	0.00			
Mean length (cm)					
Intercept	1	27394.55	27394.55	1171.77	<0.01
Season	1	369.39	369.39	15.80	<0.01
Error	28	654.60	23.38		
Total	29	1024.00			

To identify those variables responsible for these seasonal differences, the influences of precipitation and wind speed were tested using a factorial ANOVA. Neither wind speed nor the interaction between precipitation and wind speed had significant seasonal effects (Tab. 2). However, there were significant effects of precipitation on the number of species and the number and average size of fish (but not the CPUE) (Tab. 2). The changes were greatest with respect to the number and species of fish, which exhibited linear increasing trends with increasing precipitation. Changes in average length and CPUE, while significant, did not follow the same trend (Fig. 8 and 9). Although the CPUE did not vary seasonally, possibly due to the selectivity of the net, the average catch was higher in the rainy season ($p < 0.05$; Fig. 7), indicating a possible influence of precipitation on the catch. Although the variance analysis revealed significant differences in average size between seasons, the size range (20 to 44 cm) remained consistent across seasons.

The chi-square ($\chi 2$) indicated that the winds of the northeast quadrant (NE) predominated during the dry season, and the winds of the southeast quadrant (SE) predominated during the rainy season. No quadrants predominated with respect to source winds in December (i.e. during the rainy season) (Fig. 10).

The PCA clustered species into three groups (Fig. 11): Group one was associated with wind speed and consisted of *C. chrysurus*, *L. breviceps*, *C. parallelus* and *H. corvinaeformis*, with the former two species being dominant in the dry season. The second group was formed by two species: *C. crysos*, *S. brasiliensis*, *E. alletteratus*, *O. oglinum* and *L. synagris* (Fig. 11), the first three of which were dominant in the rainy season. Species of Group three were associated with areas of high precipitation and wind speed or from high turbidity waters: *C. nobilis*, *M. littoralis*, *C.*



Figures 3-4. Whittaker plot of fishes from Alagoas coast sampled during the rainy season (**3**) and the dry season (**4**).

spixii, *C. hippos*, C. *edentulus*, *B. bagre*, *M. ancylodon*; these latter two species were only recorded during the rainy season. The first two PCA axes explained 57.32 % of the total variation, with factor 1 primarily explained by precipitation (40.43 %) and factor 2 by wind speed (16.89 %) (Fig. 11). The similarity analysis revealed a significant interaction between precipitation and wind speed (ANOSIM: $r = 0.6$, $p < 0.01$). The SIMPER test identified precipitation as contributing the most to the interaction (55.67 %) and wind speed the least (0.48 %) (Tab. 3).

DISCUSSION

The results support the hypothesis that precipitation and winds are significant drivers of fish species richness and fishing yields in the coastal tropical waters. The temporal dynamics and quality of water and nutrients are ultimately affected by climate variation, especially in precipitation and wind, generating environmental conditions that can affect the structure of estuarine and marine systems (Kennedy et al. 2002) and seasonal

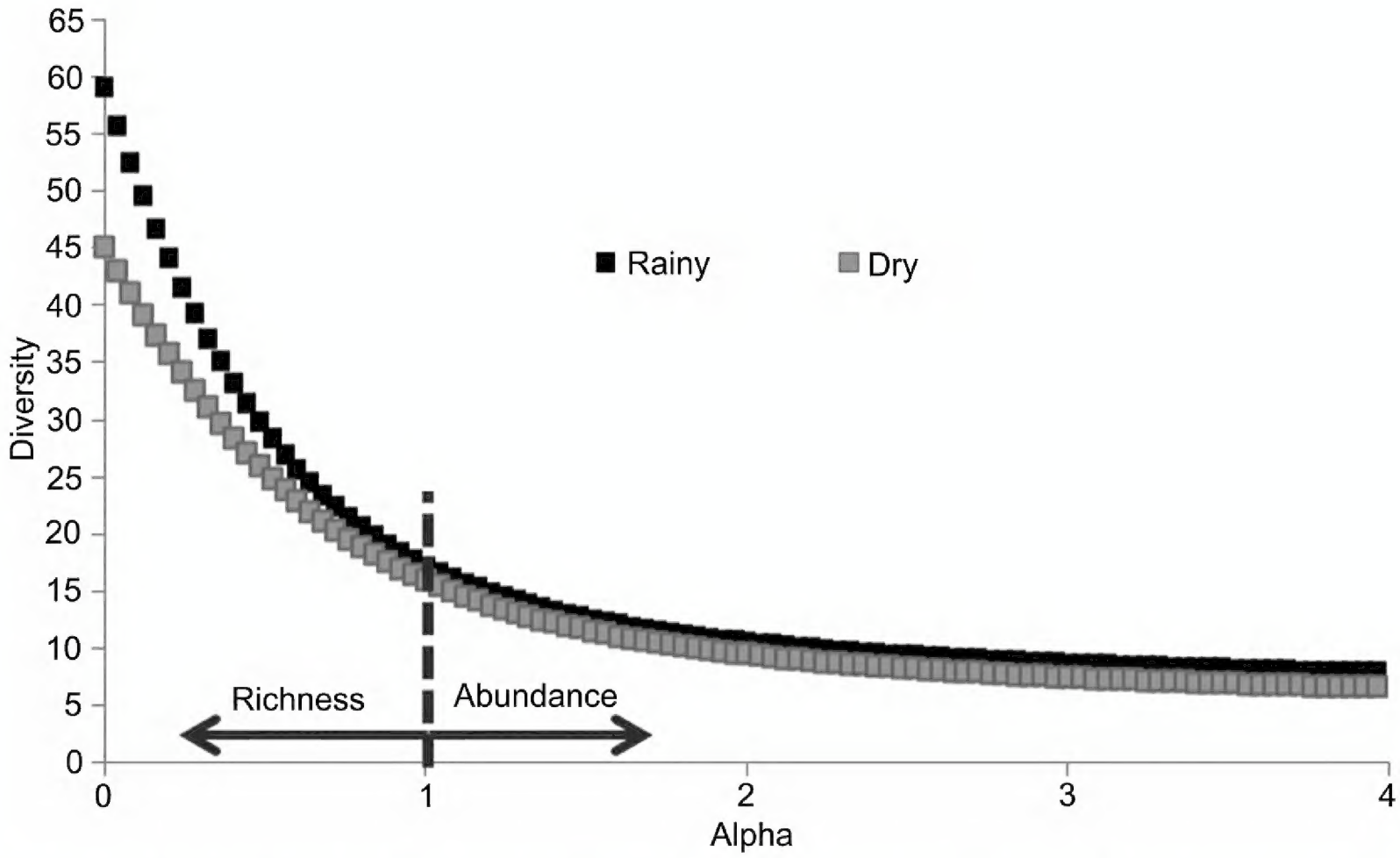


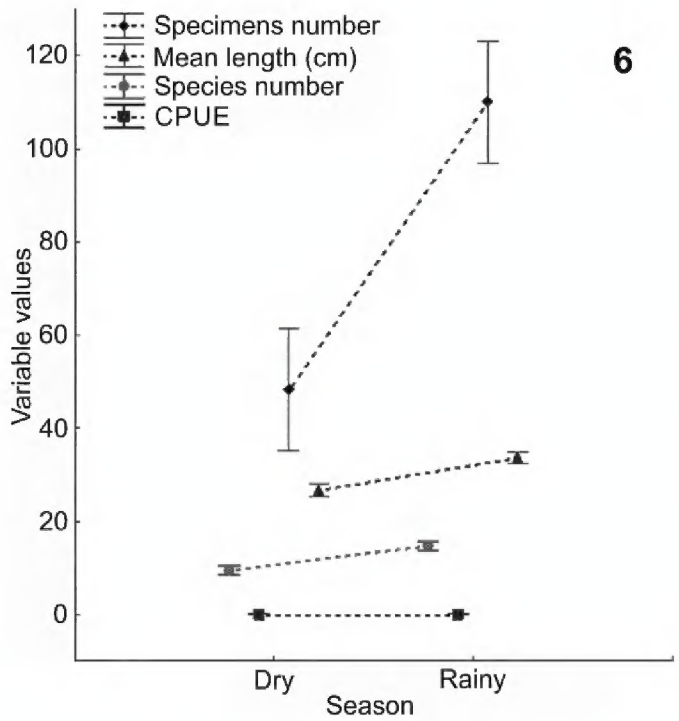
Figure 5. Diversity profile of the dry and rain seasons on the coast of Alagoas. Alpha = 1 Emphasizes the separation of richness and diversity profile.

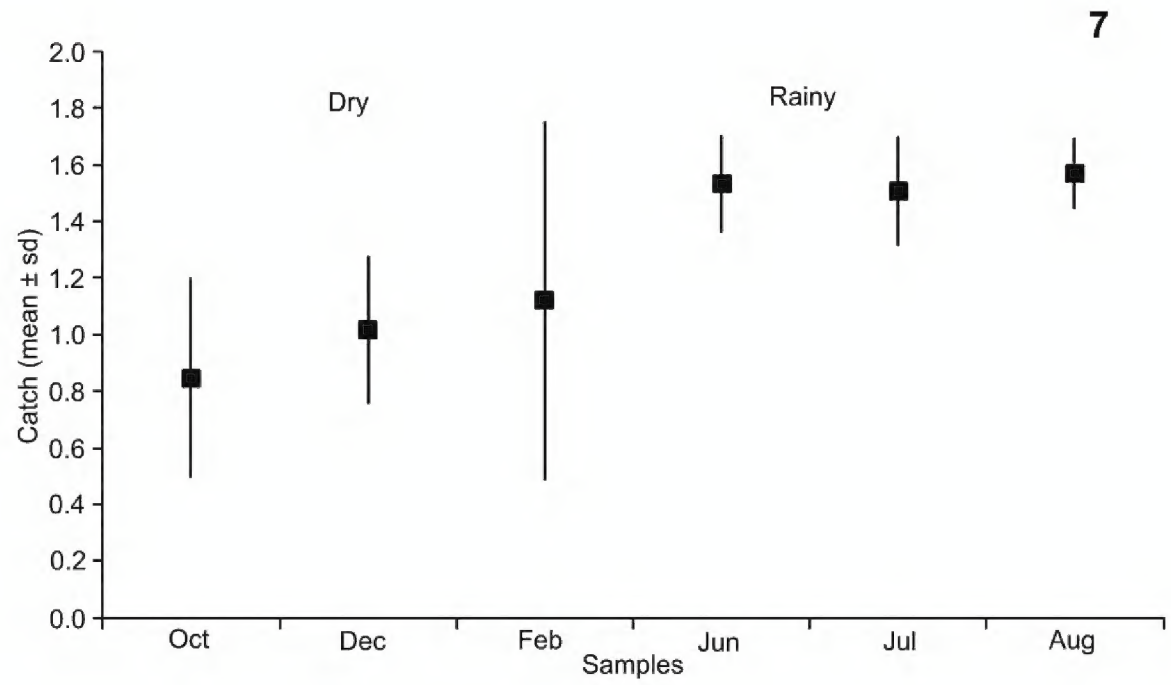
shifts in biotic responses (Lowe-McConnell 1987). In the current study, seasonal differences were observed in the number of species caught, number of individuals, CPUE and average species length. Moreover, seasonal variation in precipitation appears to influence all measures except for CPUE.

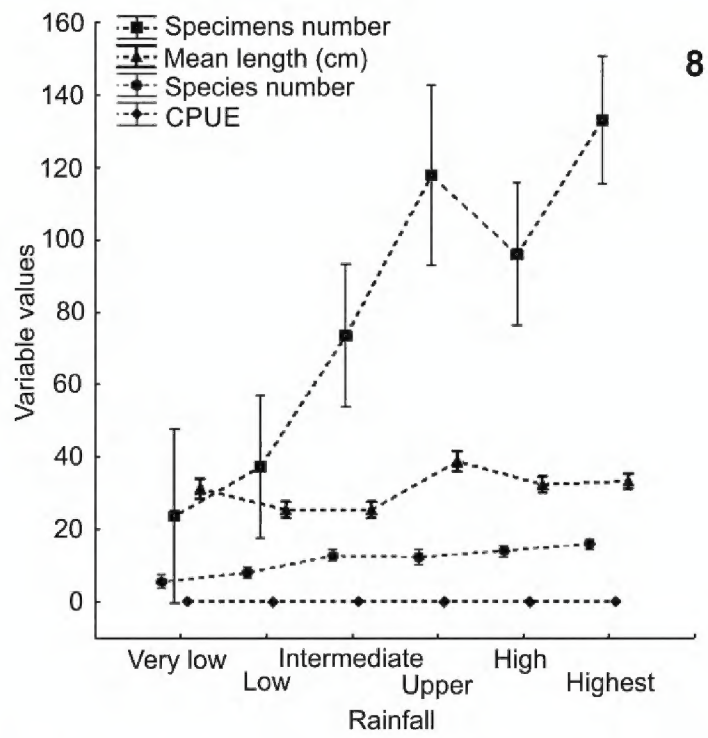
More generally, there was found that the communities sampled with a bottom gillnet off the coast of Alagoas were characterized by relatively high species richness (n = 73), corresponding to 72 % of richness as estimated by the bootstrap method. The 16 most frequent species (Suppl. material 1) belong to nine families common in several pelagic, reef and estuary regions of the eastern coast of Brazil (e.g. Araújo et al. 2002, Costa et al. 2003, Tubino et al. 2007, Lessa et al. 2009, Rangely et al. 2010, Carneiro and Salles 2011). However, the communities were dominated by few species (n = 20) that were both abundant and frequent as observed in other marine areas (e.g. Godefroid et al. 2003, Lira and Teixeira 2008).

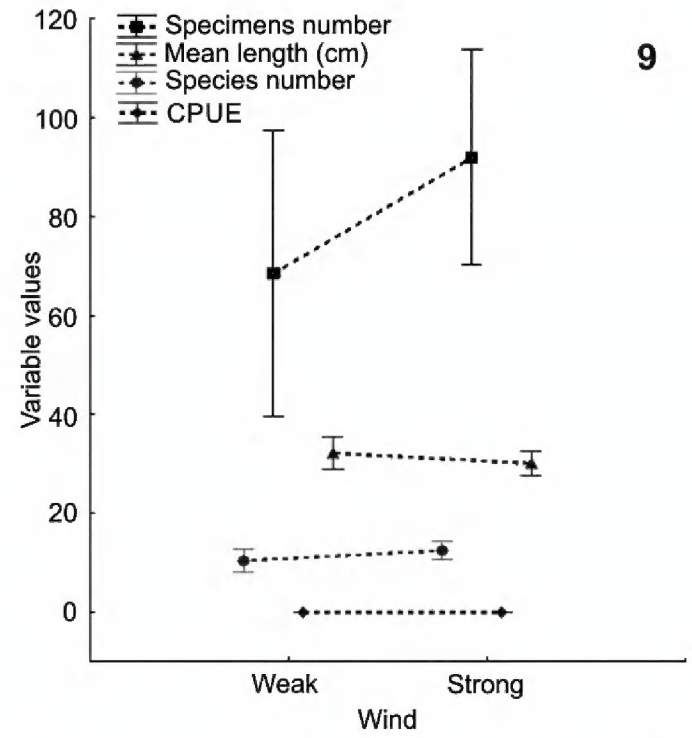
Mean yield was higher during the rainy season than during the dry season. This is not straightforward to interpret and the results of other seasonality studies vary widely with respect to periods of higher yield depending on the type of gear used, the amount of effort (Béné and Tewfik 2001, Pet-Soede et al. 2001); and the types of environments and species sampled (Jury 2011, Tubino et al. 2007). In contrast to the current study, yields were found to be higher in the dry season in the bay and estuarine environments of Rio de Janeiro, Brazil (Tubino et al. 2007) and Paranaguá Bay, southern Brazil (Vendel et al. 2003). In these regions, both primary and secondary yields and fish concentrations were higher during the dry season (Allen 1982). Despite such regional differences, Tubino et al. (2007) also reported a predominance of *C. crysos* during the dry season in tropical estuaries, when high temperatures and biological production makes these environments more attractive to enhance reproduction of marine species (Araújo et al. 1998). With respect to our data, increases in abundance and the rainy season catch could be explained by the increase in drainage (Day et al. 2012, Dittmar et al. 2001) originating from the large number of mangroves, lagoons and rivers along the Brazilian coast (Lara 2003, Araújo et al. 2006). The nutrient-rich sediments of these environments are carried to the marine environment by the rains, increasing the biological productivity of coastal waters.

The pattern of wind direction affected the seasonality of assemblage structure, with a predominance of trade winds from the northeast quadrant (NE) in the dry season and a predominance of those from the southeast quadrant (SE) in the rainy season – this is typical of regional atmospheric patterns (Servain and Legler 1986). However, as precipitation modulates seasonality in the tropics (Lowe-McConnell 1987, Macêdo et al. 2004), its effect was stronger than that of wind speed (wind speed was the least influential variable in the multivariate analysis). A weak effect of wind speed on fish assemblages were also reported for Paranaguá Bay (Vendel et al. 2003), where the highest wind speeds occurred in summer. North-eastern and south-eastern trade winds in the study region, which are associated with precipitation in the rainy season, should affect coastal currents (Hazin 2009). These currents then carry nutrients from









Figures 6–9. Mean ± sd of the number of fishes, fish total length, species richness, and CPUE by climatic seasons (**6**); CPUE (mean ± sd) by month (**7**); precipitation by month (**8**) and wind strength by month (**9**).

mangroves, lagoons and rivers to the surface and column waters of marine environments (Dittmar et al. 2001, Day et al. 2012), thereby increasing fishing yields.

Our multivariate analysis separated species into three groups. All species that were both abundant and frequent in the dry season where associated with wind. An example of this group is *L. breviceps*, a demersal species that is one of the most abundant fish on the Brazilian coast (Lira and Teixeira 2008, Souza et al. 2008). Individuals and species of the family Sciaenidae, with representatives found in all three groups were very abundant in the present work. Species of this family are very abundant along the northeastern coast (Lessa et al. 2009) and include marine, estuarine and freshwater species throughout the world (Nelson 2006).

Group two contained no estuarine resident species, only pelagic or reef species. Group two species are more flexible to environmental changes related to seasonality and its effects on marine dynamics (Longhurst and Pauly 1987a). Carangidae, Clupeidae, Scombridae, and Lutjanidae were represented in this group. Larvae of the former three families have been recorded along the north-eastern coast of Brazil (Mafalda Jr et al. 2006). The families Carangidae and Clupeidae contain many surface pelagic coastal species (Zavala-Camin 1983). Scombridae contains pelagic ocean species that use coastal waters only as nurseries (Moyle and Cech 1988). However, species of Scombridae, such as *E. alleteratus* and *S. brasiliensis* (group 2), are captured at various stages of growth in coastal areas of north-eastern Brazil (Lessa et al. 2009) due to the narrow continental shelf region. Group three contained the greatest number of species that inhabit the widest variety of habitats. It contained primarily estuarine or estuarine-dependent species, with estuarine, pelagic and reef species also present. Here, the association of the estuarine

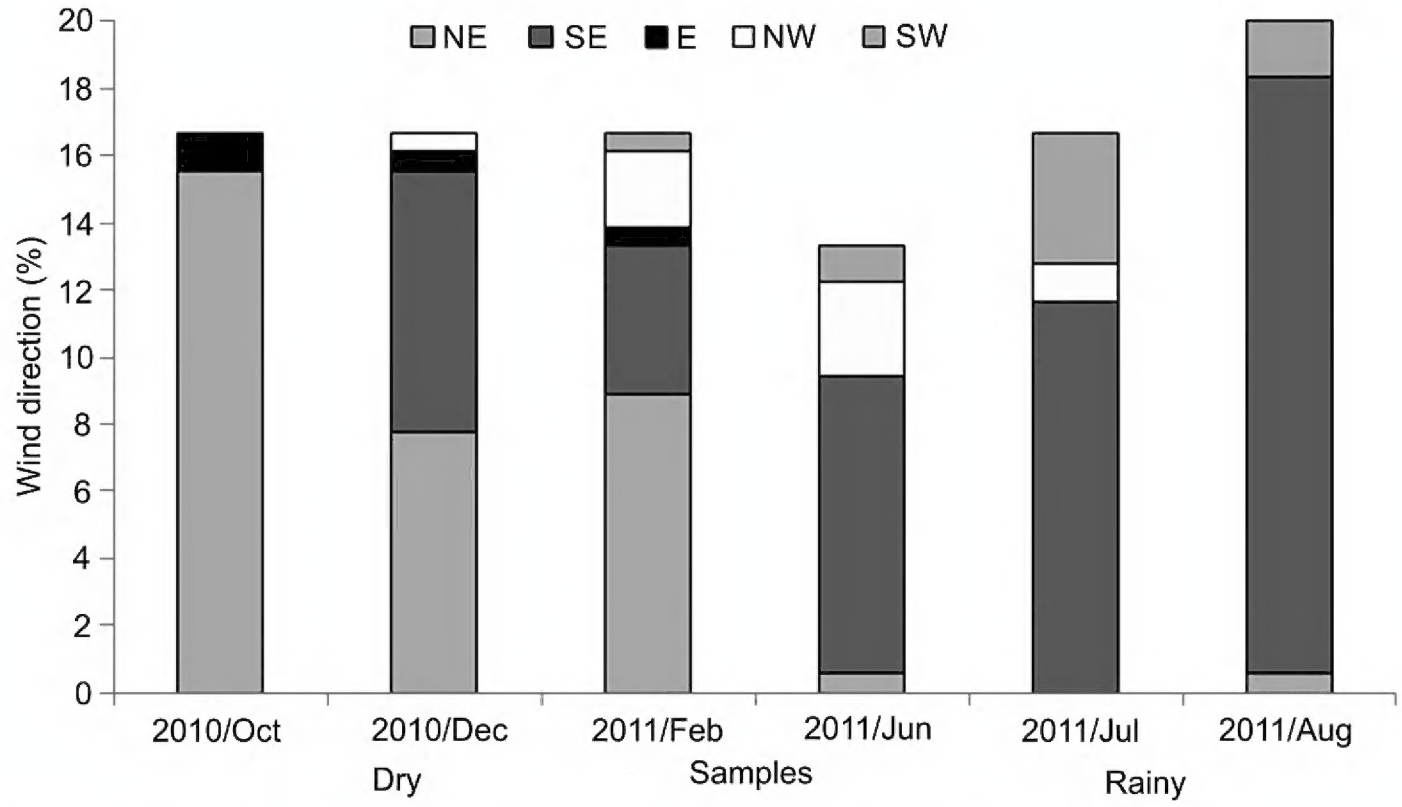


Figure 10. Frequency and direction of winds in each sampled month on the coast of Alagoas.

Table 2. Analysis of variance tables comparing effects of rainfall and winds on species number, number of fishes, CPUE and mean length for fishes caught at the coast of Alagoas.

Effect	df	SS	MS	F	p
Species number					
Intercept	1	3280.08	3280.08	281.60	<0.01
Rainfall	5	331.79	66.36	5.70	<0.01
Wind	1	26.45	26.45	2.27	0.15
Rainfall * Wind	5	84.59	16.92	1.45	0.25
Error	18	209.67	11.65		
Total	29	652.70			
Number of fishes					
Intercept	1	161309.48	161309.48	86.87	<0.01
Rainfall	5	41261.62	8252.32	4.44	0.01
Wind	1	3445.32	3445.32	1.86	0.19
Rainfall * Wind	5	17838.55	3567.71	1.92	0.14
Error	18	33422.58	1856.81		
Total	29	100360.70			
CPUE (kg)/(m*h)					
Intercept	1	0.00	0.00	38.50	<0.01
Rainfall	5	0.00	0.00	2.27	0.09
Wind	1	0.00	0.00	0.03	0.87
Rainfall * Wind	5	0.00	0.00	0.67	0.65
Error	18	0.00	0.00		
Total	29	0.00			
Mean length (cm)					
Effect	1	24276.52	24276.52	1016.97	<0.01
Intercept	5	522.17	104.43	4.37	0.01
Rainfall	1	27.11	27.11	1.14	0.30
Wind	5	144.26	28.85	1.21	0.34
Rainfall * Wind	18	429.68	23.87		
Error	29	1024.00			

Table 3. Similarity percentage analysis (SIMPER) tested for differences in the main species composition and abiotic variables (rainfall and wind strength) at the coast of Alagoas.

Variable	Contribution	%
Rainfall	34.62	55.67
Caranx crysos	3.72	61.65
Euthynnus alletteratus	3.43	67.17
Larimus breviceps	3.43	72.68
Scomberomorus brasiliensis	2.92	77.38
Conodon nobilis	1.72	80.15
Opisthonema oglinum	1.30	82.24
Chloroscombrus chrysurus	1.09	84.00
Menticirrhus littoralis	0.88	85.42
Bagre bagre	0.82	86.74
Cathorops spixii	0.71	87.88
Caranx hippos	0.70	89.01
Macrodon ancylodon	0.62	90.01
Lutjanus synagris	0.59	90.96
Centropomus parallelus	0.56	91.86
Cetengraulis edentulus	0.43	92.56
Haemulopsis corvinaeformis	0.39	93.18
Wind strength	0.30	93.66

environment with precipitation patterns and the life cycles of Neotropical species is more evident, confirming the importance of precipitation levels in influencing fish species richness and abundance in the coastal tropics.

Gillnets were chosen to collect data because they are the favored fishing method of artisanal fishers in tropical regions (Castello 2010, Godınez-Domınguez et al. 2000, Hovgård and Lassen 2000), including northeastern Brazil (Lessa et al. 2009). It also can capture several species of varying sizes(Nielsen and

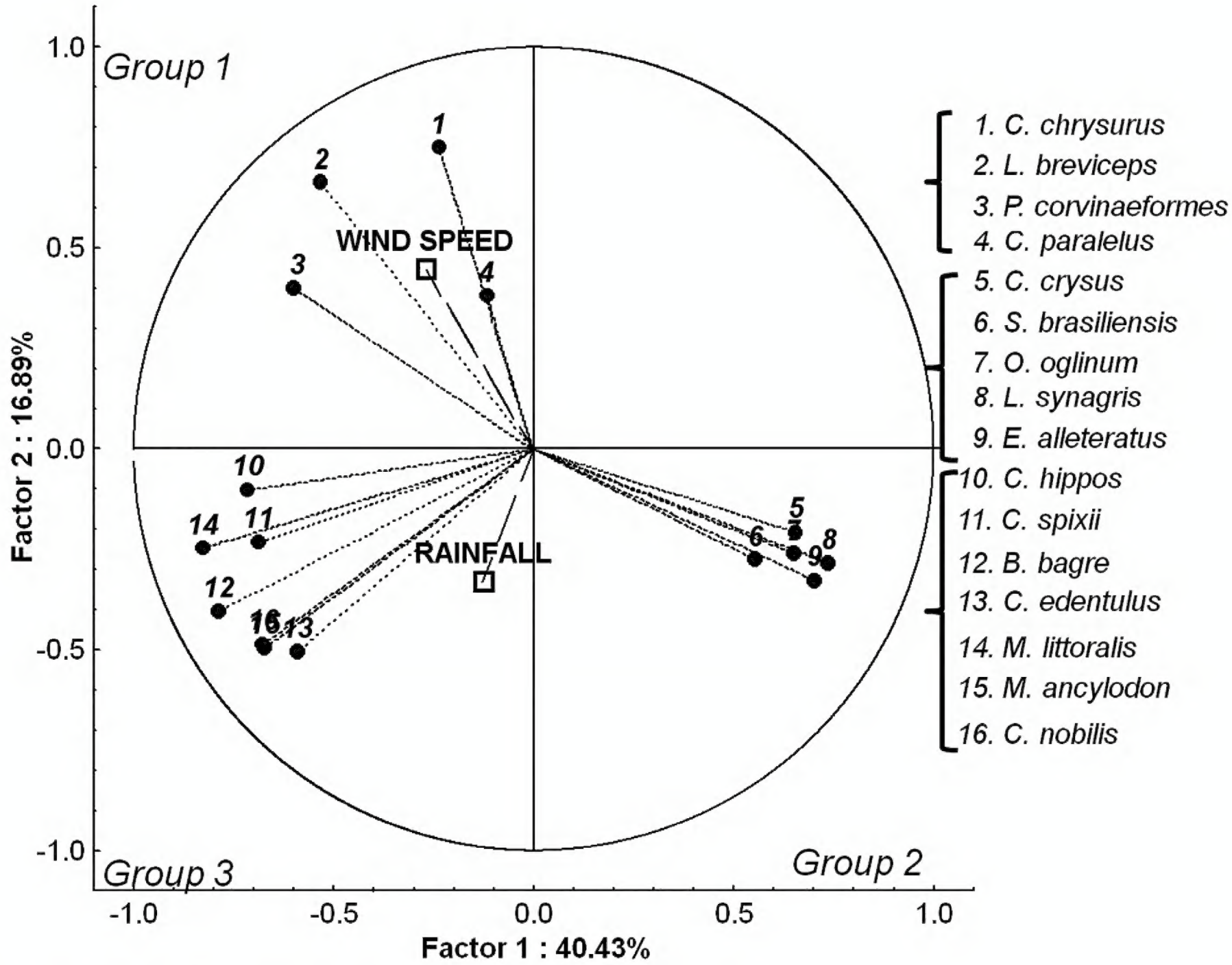


Figure 11. PCA of species abundance associated to precipitation and wind speed.

Johnson 1983), and tend to be less harmful to the aquatic environment than other methods (Hovgård and Lassen 2000). Moreover, they are also inexpensive, easy to repair and technologically simple (Hovgård and Lassen 2000).

Species co-occurrence is complex and poorly understood along neotropical waters (Andrade-Tubino et al. 2008, Azevedo et al. 2006, Barletta et al. 2010). Hidden behind precipitation and wind effects may appear the influence of trophic relationships, reproductive cycles (Keddy and Weiher 1999) and may also a stochastic component (Grossman et al. 1982). Moreover, this influence may be modulated by specific variables correlated to the rivers input into the coastal areas, including salinity, river flow (Gillson et al. 2012, Mitchell et al. 1999), turbidity (Castillo-Rivera et al. 2002, Cyrus and Blaber 1987, 1992, Johnston et al. 2007, Whitfield 1999) or pollution (Lekve et al. 2002). Nevertheless, evidences provided here indicated for consistent seasonal changes determined by precipitation and wind direction/intensity in the distribution and abundance of species within coastal fish assemblages. These ecological changes have inevitable knock-on effects on fisheries yields and the composition of the catch and should be carefully considered when developing coastal conservation, as well as for fisheries policy and regulations.

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Supplementary material 1

Taxonomic list of fish species in phylogenetic order (Nelson 2006), captured from October 2010 to August 2011 on the coast of Alagoas.

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Data type: species data

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